
ANATOMY AND HISTOCHEMICAL
LOCALIZATION OF LIPID
SECRETIONS IN BRAZILIAN
SPECIES OF *PANICUM* SECT.
LOREA (POACEAE,
PANICOIDEAE, PANICEAE)¹

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ABSTRACT

This paper constitutes the first report of the chemical nature, and histochemical localization of secretions in Brazilian species of *Panicum* L. sect. *Lorea* Zuloaga (Poaceae, Panicoideae, Paniceae); the study also includes an anatomical analysis. Lipid secretions were found in leaf sheaths and ligular regions. Lipids accumulate in specialized epidermal cells, at times surrounding the bases of the macrohairs, and in the mesophyll. Viscous secretions have been previously reported for *P. vaginiviscosum* Renvoize & Zuloaga and *P. acicularifolium* Renvoize & Zuloaga, species in section *Lorea* that are analyzed anatomically here. Lipid secretions are now also reported for the first time in eight other species of section *Lorea*: *P. bahiense* Renvoize, *P. chnoodes* Trin., *P. cipoense* Renvoize & Send., *P. durifolium* Renvoize & Zuloaga, *P. euprepes* Renvoize, *P. molinioides* Trin., *P. poliophyllum* Renvoize & Zuloaga, and *P. trinii* Kunth.

Key words: Gramineae, herbivory, lipids, *Panicum*, plant defenses, Poaceae, secreting epidermal cells.

The genus *Panicum* L., s.l., includes nearly 400 species and exhibits a worldwide distribution (Clayton & Renvoize, 1986). As presently circumscribed in its strict sense (Aliscioni et al., 2003), the genus should be limited to only subgenus *Panicum*, with five sections and approximately 100 species worldwide and 68 taxa in the Americas. The other previously considered subgenera *Dichanthelium* Hitchc. & Chase, *Megathyrsus* Pilg., *Phanopyrum* (Raf.) Pilg., and *Steinchisma* Raf. have been raised to the generic level or their species have been transferred to other genera (Zuloaga et al., 1998; Simon & Jacobs, 2003; Aliscioni et al., 2003). Also, according to Aliscioni et al. (2003), there are several species or sections of dubious taxonomic position within the Paniceae, i.e., species previously grouped in subgenus *Agrostoides* (Hitchc. & Chase ex Hsu) Zuloaga and *Phanopyrum*. Species of section *Lorea* Zuloaga (included by Zuloaga [1987] in subgenus *Phanopyrum*) are currently considered among these taxa declared *incertae sedis* (Aliscioni et al., 2003). As presently circumscribed, section *Lorea* includes 27 species, of which five are endemic to Venezuela and the Guayana Highlands;

also, 21 species are restricted to central and southern Brazil. Here they inhabit the highlands of Bahia and Minas Gerais, the cerrados (s.l.) of central Brazil to coastal regions of Rio de Janeiro and Bahia, where a few species occur in specialized cerrados, known as restingas, such as *Panicum restingae* Renvoize & Zuloaga, *P. saccolepoides* Renvoize & Zuloaga, and *P. marauense* Renvoize & Zuloaga (Zuloaga, 1987; Renvoize & Zuloaga, 1995). *Panicum chnoodes* Trin. is the only species known to be disjunct between the Guayana Highlands and central Brazil.

Panicum sect. *Lorea* is distinguished by its tussock habit, pungent leaf blades, and usually indistinct junction of sheath and blade (Renvoize, 1978; Renvoize & Zuloaga, 1984). Plants are caespitose, perennial, with basal persistent sheaths, with their blades lanceolate or linear-lanceolate, either pilose or glabrous (Renvoize & Zuloaga, 1984). The presence of viscose elements has been mentioned previously to occur in the sheaths and around the ligular region in only two species of this section, *P. vaginiviscosum* Renvoize & Zuloaga and *P. acicularifolium* Renvoize & Zuloaga (Renvoize & Zuloaga, 1995). Until now, no anatomical or histochem-

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ical studies have been made on any species of this group. We describe the anatomy of the secreting epidermal cells, and the lipid nature of their secretions is histochemically confirmed. Lipid secretions are anatomically confirmed for the first time in 10 species of *Panicum* sect. *Lorea*: *P. acicularifolium*, *P. bahiense* Renvoize, *P. chnoodes*, *P. cipoense* Renvoize & Send., *P. durifolium* Renvoize & Zuloaga, *P. euprepes* Renvoize, *P. molinioides* Trin., *P. poliophyllum* Renvoize & Zuloaga, *P. trinii* Kunth, and *P. vaginiviscosum*.

Essential oils in the Poaceae have been previously reported from roots, stems, leaves, or inflorescences of species of *Anthoxanthum* L. (= *Hierochloa* R. Br.), *Bothriochloa* Kuntze, *Chrysopogon* Trin. (= *Vetiveria* Bory), *Cymbopogon* Spreng., *Elionurus* Humb. & Bonpl. ex Willd., and *Melica* L. (Guenther, 1950; Arber, 1965; Pinder & Kerr, 1980; Watson & Dallwitz, 1992; Kaul & Vats, 1998). Most of these aromatic grasses follow the C₄ metabolic pathway of carbon fixation, and approximately 88% are members of the Andropogoneae, a tribe that spread globally by the late Miocene, possibly the period of greatest evolutionary diversity for aromatic grasses (Kaul & Vats, 1998). When ingested, these compounds slow the growth of herbivores, making them more vulnerable to predators and parasitoids (Coley & Barone, 1996), constituting a selective agent for plant defense against herbivory. Also, Ellis (1990) reported the presence of tannin-like substances in 104 species of Poaceae, with many representatives in the Andropogoneae and Arundinelleae, and occasionally in a few members of the Paniceae (two species of *Digitaria* Haller, three species of *Echinochloa* P. Beauv., and one species of *Panicum*: *P. coloratum* L.). Ellis (1990) mentioned that, chemically, tannins are a heterogeneous group of phenol derivatives.

Previous studies carried out in the Poaceae showed that secretory substances are produced and accumulated in microhairs (Amarasinghe & Watson, 1988), in the single cells adjacent to photosynthetic and non-photosynthetic tissues and between vascular bundles (Lewinsohn et al., 1998), in elaiosomes (Bresinsky, 1963; Berg, 1985; Davidse, 1987; Morrone et al., 2000), or by four different types of multicellular glands (Linder et al., 1990). The first type of multicellular gland is composed of epidermal cells forming a pad of cushion-based macrohairs (Bowden, 1971; Ellis, 1979); the second type is formed by numerous basal cells constituting the gland but not associated with macrohairs (Nicora, 1941; Davidse, 1988; Linder et al., 1990); the third type is comprised of multicellular glandular hairs (Kabuye & Wood, 1969); and the fourth type occurs as multicellular stalked glands with a central depression (Davidse, 1988; Zuloaga & Sendulsky, 1988).

Two types of glandular macrohairs were reported in *Panicum* (Kabuye & Wood, 1969): unicellular with swollen tips, present in *P. deustum* Thunb., and multicellular clavate glandular hairs, present in six species of tropical East Africa. Both types contain a yellowish and sticky substance at maturity. Multicellular glands were also reported on the lower lemma in species of *Panicum* sect. *Stolonifera* Hitchc. & Chase ex Pilg. (Zuloaga & Sendulsky, 1988), but secretory activity was not demonstrated.

The objective of this paper is to determine the nature and histochemical localization of the secretion and to describe the secretory epidermal cells in Brazilian species of *Panicum* sect. *Lorea*.

MATERIALS AND METHODS

PLANT MATERIALS

Herbarium specimens of 16 species of *Panicum* sect. *Lorea* were studied in order to detect specialized secreting epidermal cells (see Appendix 1).

ANATOMICAL STUDIES

Sheaths and blades were fixed in FAA (1 formalin: 4 alcohol 96%: 1 acetic acid) for 48 hours, and then stored in 70% ethanol, or they were removed from herbarium specimens and rehydrated in 5% Contrad 70 (Decon Laboratories, King of Prussia, Pennsylvania, U.S.A.) (Schmid & Turner, 1977) over 24 hours at 20°C. The material was desilicificated in hydrofluoric acid (5%) for 24 hours. Then the material was washed in distilled water, dehydrated in an ethanol series, and embedded in paraffin. Transverse and longitudinal sections 10 µm thick were cut on a rotary microtome. Sections were double stained with safranin-fast green.

Preliminary observations of the leaf material stained with Sudan IV (Gahan, 1984) showed that they are rich in lipids. Stained transversal sections of the leaf sheath were analyzed to detect and determine the localization of lipid secretions in the different tissues. We used only herbarium material for this study.

Light microscope (LM) studies were made using a ZEISS Phomi III microscope (Zeiss, Oberkochen, Germany), with a 35 mm photographic camera and Kodak (Rochester, New York, U.S.A.) Gold ASA100 film.

For observation with SEM, pieces of the middle portion of the leaf sheaths were mounted on stubs, carbon coated in a vacuum evaporator, and coated with a palladium alloy. The observations were made using a ZEISS DSM 940 A microscope at the Instituto de Botánica Darwinion, Argentina. Complementary observations of secretory structures were made with an

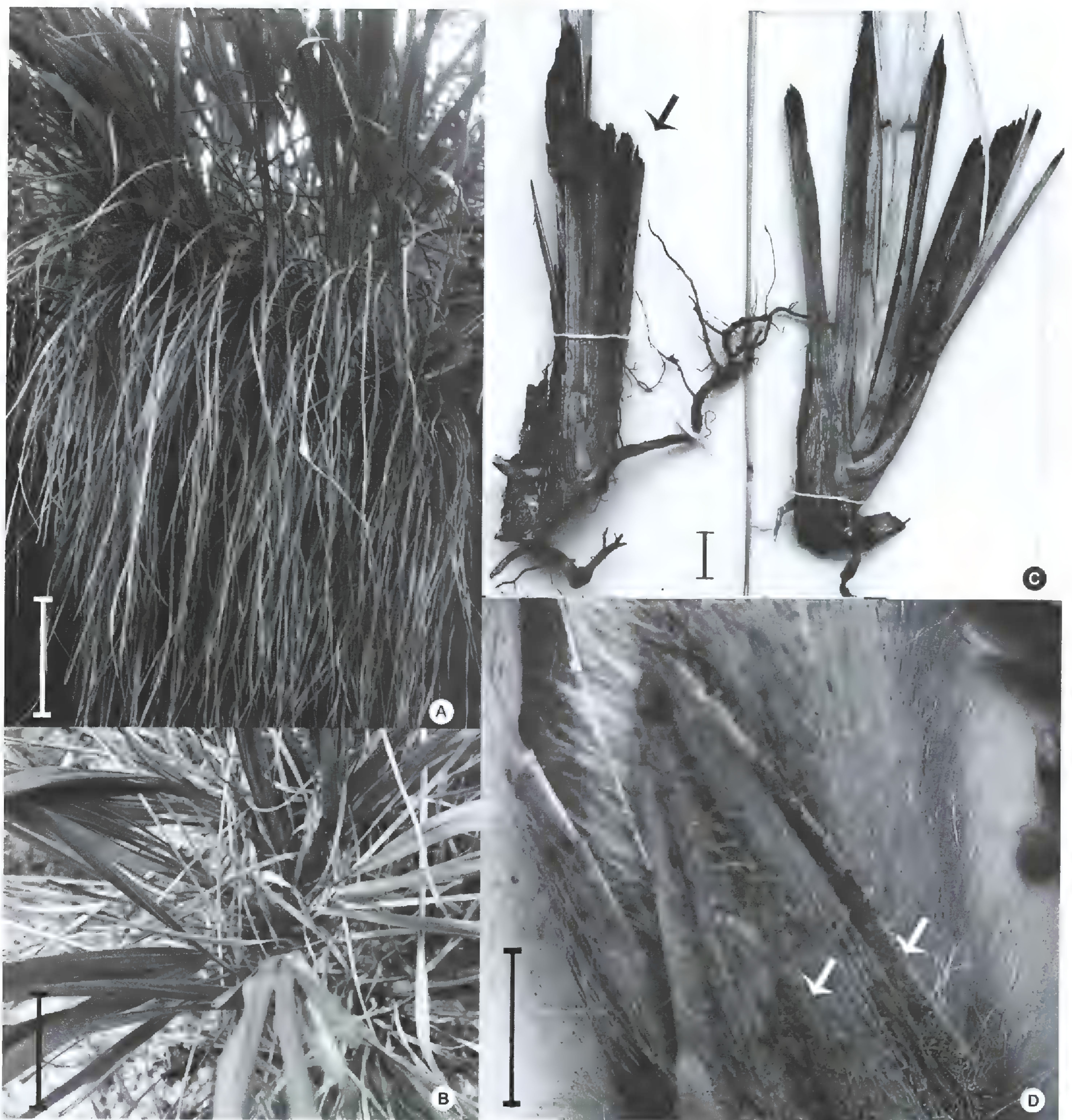


Figure 1. —A. *Panicum poliophyllum* growing in Caraça, Minas Gerais, Brazil. —B. Base of the plant of *P. poliophyllum*, showing dry leaf sheaths and young innovations. —C. Herbarium specimen of *P. subtiramulosum* (Caraça, Minas Gerais, Brazil: Fonseca & Alvarenga 2109, SI) showing evidences of fire (arrow). —D. Herbarium specimen of *P. bahiense* from Bahia, Brazil (Zuloaga et al. 4850, SI), with secretory structures (arrows) in the cataphyll. Scale bars: A, B = 10 cm; C = 1 cm; D = 0.5 cm.

environmental SEM in an XL30 ESEM (Phillips, Eindhoven, The Netherlands) at the Instituto Nacional de Tecnología Industrial (INTI), Argentina.

RESULTS

FIELD OBSERVATIONS

Plants of *Panicum* sect. *Lorea* collected from Brazil grow in campos rupestres, rocky grasslands, at 1070–1600 m. In all of the examined material, the distal culms, covered with young leaves, are protected by

abundant and dry basal sheaths, constituting an important source of combustible material during fires in the cerrado landscape (Fig. 1A, B). In some herbarium specimens, burned leaf remains can be readily observed, and burning is a regular phenomenon in cerrado environments in central Brazil. When these grasses are burned, young culms are protected at their base by cataphylls and remnants of basal burned sheaths (Fig. 1C, D).

Field observations of some species of *Panicum* sect. *Lorea* showed the presence of large amounts of sticky secretions, with a strong and disagreeable smell.

Table 1. Localization of lipid secretions for 10 of the 16 species investigated in *Panicum* sect. *Lorea* with Sudan IV in transverse sections of leaf sheath. + = present, – = absent.

Species	Sheath indumentum	Mesophyll	Epidermis		Specialized secreting structures
			Abaxial	Adaxial	
<i>P. acicularifolium</i>	villous	+	+	+	
<i>P. bahiense</i>	villous	+	+	++	+ (unicellular)
<i>P. chnoodes</i>	villous	+	+	++	
<i>P. cipoense</i>	villous	+	+	–	–
<i>P. durifolium</i>	villous	+	+	++	–
<i>P. euprepes</i>	subglabrous	+	+	+	+ (unicellular)
<i>P. molinioides</i>	villous	+	++	+	+ (multicellular)
<i>P. poliophyllum</i>	subglabrous	+	+	–	+ (unicellular)
<i>P. trinii</i>	villous	+	+	++	
<i>P. vaginiriscosum</i>	subglabrous	+	+	++	

These secretions are restricted to leaf sheaths and ligular regions, which turn viscid. Usually, secretions are more abundant in cataphylls (Fig. 1D) and basal sheaths while young plants are growing, but they are almost absent in upper leaf sheaths. Basal sheaths are strongly attached to the culms, and marginal hairs are impregnated with sticky secretions that enhance the adhesion of sheaths to the culms.

ANATOMICAL STUDIES

Basal sheaths are villous all over or pilose on the margins and subglabrous on the surface (Table 1). Species in *Panicum* sect. *Lorea* with villous basal

sheaths, e.g., *P. acicularifolium*, *P. bahiense*, *P. chnoodes*, *P. cipoense*, *P. durifolium*, *P. molinioides*, and *P. trinii*, show conspicuous costal and intercostal zones (Fig. 2A). Macrohairs are restricted to intercostal areas (Fig. 2A–C) and are unicellular, stiff, with slightly thickened walls, and their bases are sunken and surrounded by a group of secreting epidermal cells slightly raised above the general level of the sheath surface (Fig. 2C). This type of macrohair is known as a cushion hair (Metcalf, 1960; Ellis, 1979).

Species in *Panicum* sect. *Lorea* with subglabrous basal sheaths as in *P. euprepes*, *P. poliophyllum*, and *P. vaginiriscosum* show few undulations associated with vascular bundles. Solitary or grouped secreting

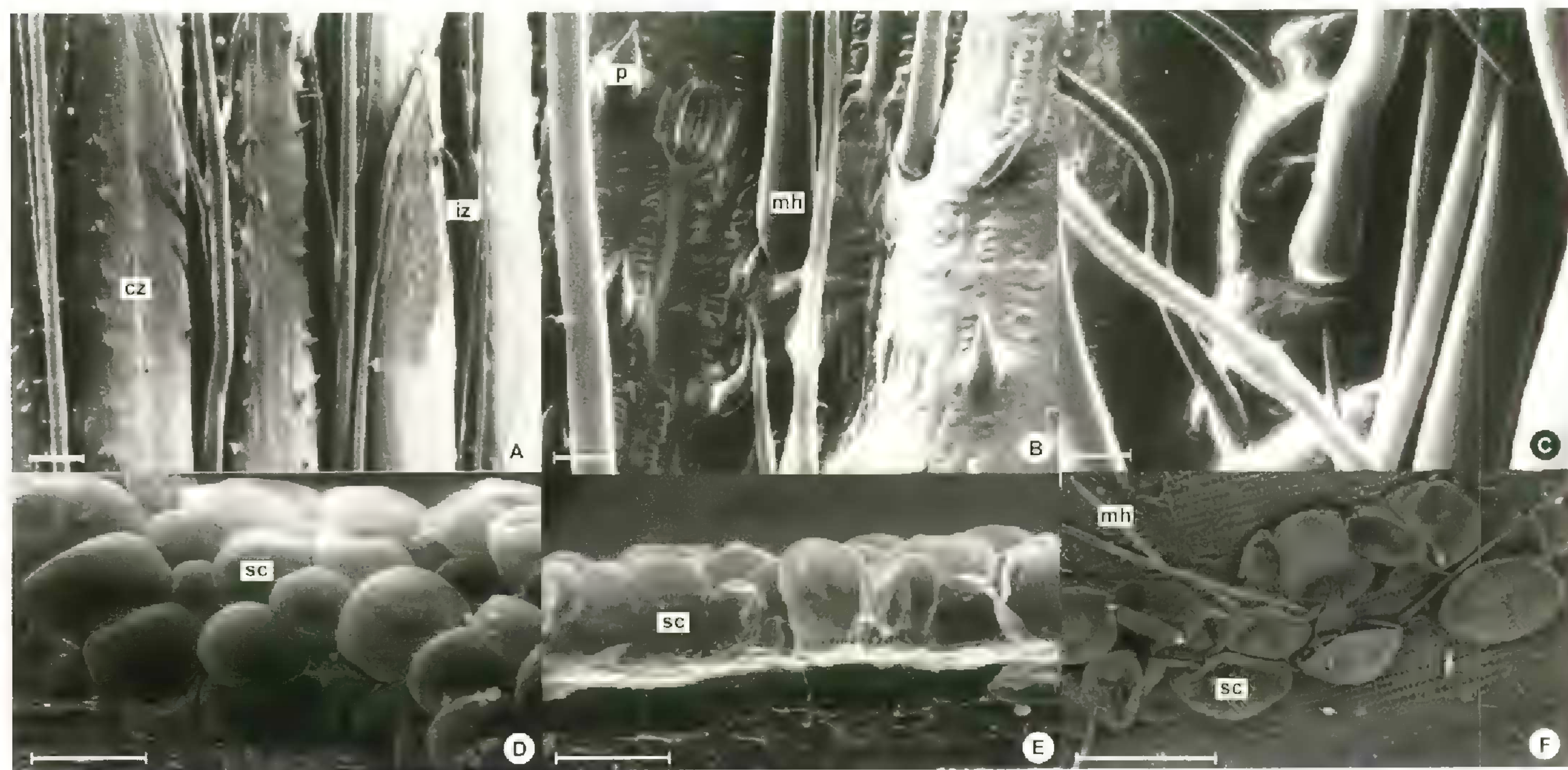


Figure 2. SEM microphotographs of the leaf sheath in *Panicum* sect. *Lorea*. —A. General view of the abaxial surface showing the position of macrohairs at intercostal zones. —B. Macrohairs with specialized epidermal cells in young leaf sheaths. —C. Macrohairs with collapsed, specialized epidermal cells after secretion in mature leaf sheaths. —D, E. Groups of specialized epidermal cells. —F. Groups of specialized epidermal cells after secretion. A, B, D–F: *P. euprepes* (Zuloaga et al. 4783, SI); C: *P. vaginiriscosum* (Zuloaga et al. 4781, SI). cz, costal zone; iz, intercostal zone; mh, macrohairs; p, prickle; sc, specialized epidermal cells. Scale bars: A–C = 20 μ m; D, E = 100 μ m; F = 200 μ m.



Figure 3. LM photographs of the leaf sheath in *Panicum* sect. *Lorea*. —A. Transverse section stained with Sudan IV. —B. Active cells stained with Sudan IV. Note elaioplasts at arrow. —C. Inactive and lignified cells, staining negatively to Sudan IV. D. E. Active cells stained with safranin-fast green. —D. Transverse section. —E. Longitudinal section. —F. Multicellular-secreting structures in leaf sheath transverse section. —G. Detail of a multicellular-secreting structure in leaf sheath transverse section. A: *P. vaginiviscosum* (Zuloaga et al. 4781, SI); B–E: *P. euprepes* (Zuloaga et al. 4783, SI); F–G: *P. molinioides* (Zuloaga & Morrone 4701, SI). ab, abaxial epidermis; ad, adaxial epidermis; e, elaioplast; me, mesophyll; mx, metaxylem; ph, phloem; s, sclerenchyma; sc, specialized epidermal cells; vb, vascular bundles; x, xylem. Scale bars: A–F = 100 μ m; G = 50 μ m.

specialized epidermal cells are present in both surfaces, although they are more frequent on the abaxial surface and often surround the bases of the macrohairs (Fig. 2D–F). These cells are not so abundant, although secretions are detected in fresh and herbarium material.

All species examined in transverse section show a unistratified epidermis composed of quadrangular to

tabular cells (Fig. 3). On both surfaces, the epidermal cells have a thick outer tangential cell wall. The chlorenchyma has isodiametric to irregularly shaped cells. In viscid sheaths, only mesophyll cells contain abundant elaioplasts with lipids. The sclerenchyma is subepidermic and discontinuous, and forms adaxial and abaxial girders associated with primary and secondary vascular bundles. Fibers are lignified.

Transverse sections of the leaf sheaths observed from herbarium material of *Panicum* sect. *Lorea* show a positive reaction to Sudan IV. Lipids are accumulated in the mesophyll and also in the xylem and phloem parenchyma of the vascular bundles (Fig. 3A). Lipids are especially abundant inside the specialized epidermal cells (Fig. 3B). However, we did not observe specialized pores through which lipids are secreted. Specialized epidermal cells, once transformed in inactive cells, are persistent on the sheath surface and easily detected under magnification by their lignified and brownish-colored walls (Fig. 3C).

In transverse and longitudinal sections of the leaf sheaths, specialized secretory epidermal cells are globose to claviform in shape, according to their density on the surface (Fig. 3D, E). Their walls are thin and lignified, apparently not interrupted by specialized pores. The epidermal origin of these secreting cells is clearly demonstrated. The cytoplasm of these cells is dense, with abundant vesicles of different sizes. The nucleus is prominent and of variable placement with one or two visible nucleoli (Fig. 3D, E).

The presence of lipids was detected in 10 species: *Panicum acicularifolium*, *P. bahiense*, *P. chnoodes*, *P. cipoense*, *P. durifolium*, *P. euprepes*, *P. molinioides*, *P. poliophyllum*, *P. trinii*, and *P. vaginiviscosum* but not in the remaining six analyzed in section *Lorea*: *P. animarum* Renvoize, *P. lagostachyum* Renvoize & Zuloaga, *P. loreum* Trin., *P. lutzii* Swallen, *P. restingae*, and *P. subtiramulosum* Renvoize & Zuloaga. Lipids were detected in mesophyll and both epidermides with different accumulations in the adaxial and abaxial surfaces according to the species (Table 1). Lipids appear abundant on adaxial epidermis of *P. bahiense*, *P. durifolium*, *P. trinii*, and *P. vaginiviscosum*. The presence of unicellular specialized epidermal cells was observed in *P. bahiense*, *P. euprepes*, and *P. poliophyllum*. In *P. bahiense*, specialized secretory cells are distributed in intercostal zones and are associated with macrohairs. *Panicum molinioides* possesses multicellular secretory structures distributed in abaxial costal and intercostal zones that are generally not associated with macrohairs. In *P. molinioides*, glands are composed of a group of cells with a slightly concave central area. In transverse sections, these cells are axially elongated and are all surrounded by a distinct and thick cuticle (Fig. 3F, G).

DISCUSSION

Fire has occurred in tropical savannas for thousands of years, shaping the landscape and selecting for adapted flora and fauna (Ramos Neto & Pivello, 2000). Many studies have concentrated on how plant

species adapt to fire in the Brazilian cerrados (Coutinho, 1990). However, the herbaceous layer of the cerrado has not been studied as intensively as the woody layer (Mistry, 1998), and more knowledge is needed about the mechanism put in place in native herbaceous plants to survive herbivory after fire.

The tropical humid climate of the cerrado region has a dry winter when grasses dry out, and a wet summer. The burning season occurs from May to September, when the herbaceous vegetation is dry and more flammable. In the early wet season (September–October), fire occurrences decrease, although the vegetation is still capable of maintaining a fire (Ramos Neto & Pivello, 2000). Soils under cerrado vegetation are generally very poor in mineral nutrients, with toxic levels of aluminum and high acidity (Coutinho, 1982). After fires, the ash is highly beneficial to the growth of herbaceous and undershrub plants with superficial root systems, since they are provided with a large quantity of mineral nutrients and a significant reduction in aluminum toxicity (Coutinho, 1990). The ground layer plants are xeromorphic, usually with rather stiff leaves with smooth or harsh surfaces, although some grasses and forbs have soft, hairy leaves (Eiten, 1982).

Plants growing in a cerrado sensu stricto (with tree and scrub forms, where trees do not form a continuous canopy, Eiten, 1982) are mostly perennials, have a gray and dusty appearance, and possess hard siliceous leaves, sometimes even densely hairy, and with underground organs well adapted to burning. Furthermore, in species of *Panicum* sect. *Lorea*, basal sheaths are strongly attached to the culms, and marginal hairs are impregnated with sticky secretions, enhancing the adhesion of sheaths to the culms. These characteristics may represent a strategy to decrease the entrance of insects inside the leaf sheath, and perhaps also to reduce dehydration and combustibility. Fresh green leaves are produced shortly after burning; intense flowering can also be observed a few days or weeks after cerrado fires (Coutinho, 1982; Silberbauer-Gottsberger, 1984; Miranda et al., 2002). According to Marquis et al. (2002), a peak in herbivore abundance is associated with the flush of new leaves during the initial part of the wet season. Furthermore, cerrado plants most commonly attacked by insects can evade these herbivores by evolving chemically novel toxins as deterrents to distinguish themselves from their neighbors (Marquis et al., 2002). Ellis (1990) postulated that the presence of tannin-like substances (TLS) in species of grasses is primarily associated with sour grasslands and savannas of southern Africa, and that this feature may be related to a chemical defense mechanism as a response to damage caused by herbivores.

In species of *Panicum* sect. *Lorea*, the production of lipids, combined with a repellent substance, might well be associated with the sprouting of fresh green leaves, making the foliage unpalatable for grazing animals or predators. That association would account for the occurrence of secreting cells only on the cataphylls, leaf sheaths, and ligular regions of basal foliage, but not in leaves of the upper culms. In 10 of the 16 analyzed species of section *Lorea*, of a total of 27 species included in this section, lipid secretions are concentrated in epidermal cells, especially at the bases of the macrohairs, and in mesophyll. Globose-secreting cells are not so abundant, although secretions were detected in fresh material during fieldwork and in herbarium material. Although the presence of sticky substances and specialized secreting epidermal cells was not detected in three of the studied species of this section, the vast majority contained both and are likely to occur in other unstudied taxa of section *Lorea*. In general, species of this section occur in areas seldom visited by botanists, making collections scarce (Renvoize, 1978), but it is important to collect them with the complete basal portion to locate secretory structures or substances.

We have shown that the analyzed species of *Panicum* sect. *Lorea* have important differences in the presence and type of secretory structures. Lipids are present in the epidermis and mesophyll in 10 of the 16 species studied. Specialized cells are present or absent and, when present, are unicellular or grouped in multicellular structures.

Little information has been published in relation to interactions among other genera of lipid-secreting grasses and herbivores. In some species of the genus *Pentaschistis* (Nees) Spach inhabiting southern Africa and Madagascar, shoots are aromatic (or fetid) due to the presence of multicellular glands at the base of the macrohairs on the abaxial leaf blade surface, sheaths, pedicels, or glumes (Linder et al., 1990; Watson & Dallwitz, 1992). Plants, such as species of *Priocanthium* Desv., that are sticky and/or produce an unpleasant smell originating from an unknown volatile substance, are postulated to have an anti-herbivore mechanism (Davidse, 1988). Furthermore, a similar type of macrohair to that described in some species of *Panicum* sect. *Lorea* was reported in *Andropogon gayanus* Kunth var. *bisquamulatus* (Hochst.) Hack. (Andropogoneae) by Bowden (1971), but this author interpreted that the epidermal cells that surround macrohair bases are nectaries.

Most of the aromatic grasses studied up to the present are Andropogoneae and follow the C₄ pathway of carbon fixation (Kaul & Vats, 1998). The genus *Panicum*, s.l., includes all photosynthetic types: C₃, C₄ (NAD malic enzyme [NAD-ME], phosphoenolpy-

ruvate carboxykinase [PCK], or NADP malic enzyme [NADP-ME]), and also C₃/C₄ intermediate species. This analysis shows that many species of *Panicum* sect. *Lorea*, which includes only C₃ species, have essential oils. Aliscioni et al. (2003) have suggested that *Panicum* sect. *Lorea* should be segregated from *Panicum*, because the species of this section that were studied were placed in an independent and strongly supported clade separate from *Panicum* s. str. As previously mentioned, species of this section share a similar habitat and distribution, as well as a suite of morphological characters. The presence of secretory tissue in species of this section may represent another unique character for this group. Nevertheless, the presence of secretory tissues should be analyzed in more species of *Lorea* and in new material of those species where glands were not found in this study, to confirm if this character represents a distinguishing feature for the group.

ADDENDUM

While this paper was in press, a new contribution (Sede et al., 2008) presented a phylogenetic analysis of section *Lorea*, which led to the segregation of two new genera in the Paniceae. Species discussed here were rearranged in both *Apochloa* Zuloaga & Morrone and *Renvoizea* Zuloaga & Morrone.

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APPENDIX 1. Herbarium specimens of *Panicum* sect. *Lorea* species studied to detect specialized secreting epidermal cells.

- P. acicularifolium* Renvoize & Zuloaga. BRAZIL. Bahia: Mun. Rio de Contas: Pico das Almas, vertente leste, subida do pico do campo do Queiroz, *Harley et al.* 26321 (isotype, SI).
- P. animarum* Renvoize. BRAZIL. Bahia: Mucugé, *Giulietti et al.* 1537 (SI); Mun. Rio de Contas, subida a Pico das Almas, 13°35'S, 41°41'W, 1450 m, 15 Feb. 1994, *Zuloaga et al.* 4848 (SI).
- P. bahiense* Renvoize. BRAZIL. Bahia: Mun. Rio de Contas, subida a Pico das Almas, *Zuloaga et al.* 4850 (SI).
- P. chnoodes* Trin. BRAZIL. Minas Gerais: Serra do Cipó, entre Posta Palacio e Morro do Pilar, *Vidal* 5996 (SI).
- P. cipoense* Renvoize & Send. BRAZIL. Minas Gerais: Rodovia de Cardeal Mota a Conceição do Mato Dentro, BR-010, Serra do Cipó, Km 118, *Zuloaga & Morrone* 4694 (SI); Mpio. Jaboticatubas, ao longo da rodovia Lagoa Santa, Conceição do Mato Dentro, Diamantina, *Sendulsky et al.* 389 (paratype, SI).
- P. durifolium* Renvoize & Zuloaga. BRAZIL. Bahia: Mun. Rio de Contas: 11 km ao N da cidade na estrada para o

povoado de Mato Grosso, 13°30'S, 41°52'W, *Harley et al.* 26053 (isotype, SI).

P. euprepes Renvoize. BRAZIL. Bahia: Mun. Palmeiras, Pai Inacio, Morro do Pai Inacio, campo rupestre, *Zuloaga et al.* 4783 (SI). Minas Gerais: Mun. Jaboticatubas, Km 115 ao longo da rodovia Lagoa Santa–Conceição do Mato Dentro–Diamantina, *Joly et al.* 861 (SI); Rodovia de Cardeal Mota a Conceição do Mato Dentro, BR-010, Serra do Cipó, Km 118, *Zuloaga & Morrone* 4696 (SI).

P. lagostachyum Renvoize & Zuloaga. BRAZIL. Bahia: Morro do Chapéu, *Pereira* 2139 (SI).

P. loreum Trin. BRAZIL. Minas Gerais: Rodovia de Cardeal Mota a Conceição do Mato Dentro, BR-010, 22–24 km de Cardeal Mota, *Zuloaga & Morrone* 4597 (SI); Mpio. de Jaboticatubas, ao longo da rodovia Lagoa Santa–Conceição do Mato Dentro–Diamantina, *Sendulsky et al.* 448 (SI).

P. lutzii Swallen. BRAZIL. Rio de Janeiro: Pedra Bonita, *Castellanos s.n.* (SI).

P. molinioides Trin. BRAZIL. Minas Gerais: Rodovia de Cardeal Mota a Conceição do Mato Dentro, BR-010, Serra do Cipó, Km 121, *Zuloaga & Morrone* 4701 (SI).

P. poliophyllum Renvoize & Zuloaga. BRAZIL. Minas Gerais: Serra de Ouro Branco, *Zuloaga s.n.* (SI).

P. restingae Renvoize & Zuloaga. BRAZIL. Espírito Santo: Guarapari, Km 32 da ES060–Setiba, *Silva* 579 (SI).

P. subtiramulosum Renvoize & Zuloaga. BRAZIL. Distrito Federal: Reserva Ecol. do IBGE, próximo ao Córrego Taquara, *Fonseca & Alvarenga* 2109 (SI); APA Gama–Cabeça de veado, Cristo Redentor, *Filgueiras & Zuloaga* 2132 (SI).

P. trinii Kunth. BRAZIL. Bahia: Mun. Rio de Contas: Pico das Almas, vertente leste, Campo do Queiroz, *Harley et al.* 26662 (CEPEC); Pico das Almas, vertente leste, na parte N do vale abaixo do pico, *Harley et al.* 26203 (SI); Distrito de Serra Grande, Itacaré estrada que liga Serra Grande, ramal 13 que leva ao Campinho Cheiroso, *Amorim et al.* 727 (CEPEC). Distrito Federal: Restinga de Jacarepaguá, *Duarte* 5014 (SI).

P. vaginiviscosum Renvoize & Zuloaga. BRAZIL. Bahia: Mun. Ilheus, ruta de Olivença a Una, 17 km de Olivença, en borde de selva, *Zuloaga et al.* 4853 (SI); Mun. Palmeiras, Pai Inacio, Morro do Pai Inacio, campo rupestre, *Zuloaga et al.* 4781 (SI); Mun. Rio de Contas, Pico das Almas, vertente leste, Trilho Faz. Silvina-Queiroz, *Harley et al.* 25772 (isotype, SI).